

A REVIEW OF THE NEOTROPICAL GENERA *AMALOPHYLLON*, *NIPHAEA*, AND *PHINAEA* (GESNERIACEAE-GLOXINIEAE)

JOHN K. BOGGAN*

National Museum of Natural History, Dept. of Botany, Smithsonian Institution,
Washington, DC 20013-7012, USA. Email: bogganj@si.edu

LAURENCE E. SKOG

National Museum of Natural History, Dept. of Botany, Smithsonian Institution,
Washington, DC 20013-7012, USA; Marie Selby Botanical Gardens, Sarasota, FL 34236-7726, USA.

ERIC H. ROALSON

School of Biological Sciences and Center for Integrated Biotechnology, Washington State
University, Pullman, WA 99164-4236, USA.

ABSTRACT. Previous molecular and morphological studies have revealed that the genus *Phinaea* (Gesneriaceae-Gloxinieae) as circumscribed until now is polyphyletic. On the basis of these studies *Phinaea* s.s. is restricted to three species. *Amalophyllon*, originally described in Scrophulariaceae, is here recognized as a member of Gesneriaceae and as the first available generic name for the majority of the species previously included in *Phinaea*. An emended description of *Amalophyllon* is provided and the frequently confused genera *Amalophyllon*, *Phinaea*, and *Niphaea* are contrasted and the differences between them clarified. Eight species are transferred to *Amalophyllon*: *A. albiflorum*, *A. caripense*, *A. divaricatum*, *A. laceratum*, *A. macrophyllum*, *A. repens*, *A. roezlii*, and *A. rubidum*. Lectotypes are designated for two names, *Niphaea parviflora* and *Napeanthus repens*. Three new species, *Amalophyllon clarkii*, *A. macrophyloides*, and *Niphaea pumila*, are described. A key to the genera and species and lists of the currently known taxa for all three genera are provided.

Key words: Gesneriaceae, Gesnerioideae, Gloxinieae, Scrophulariaceae, *Amalophyllon*, *Niphaea*, *Phinaea*

INTRODUCTION

The neotropical genera *Niphaea* Lindl. and *Phinaea* Benth. comprise species of small herbs with subrotate white corollas and have been confused through much of their taxonomic history. Lindley (1841, 1842) described *Niphaea* with a single species, *N. oblonga* Lindl., and several additional species were subsequently described by other authors. Bentham (1876) segregated in the new genus *Phinaea* several of these species that differed from *N. oblonga* in having stamen filaments longer (rather than shorter) than the anthers and anther cells with distinct (as opposed to confluent) locules. On the basis of these characters, most *Niphaea* species were subsequently transferred to *Phinaea* (Hemsley 1882, Fritsch 1893–1894, Solereder 1909, Morton 1957). Other species transferred to *Phinaea* were originally described in the genera *Trevirana* Willd. (Poeppig 1840) and *Napeanthus* Gardner (Donnell Smith 1901, Brandegee 1914). Although the distinction between *Niphaea* and *Phinaea* was discussed at length by Solereder (1909), the two genera have remained confused

and the taxonomic affinity of several taxa has remained uncertain. Morton (1937) observed, “*Phinaea* is one of the least known genera of Gesneriaceae. Seven species have been described, but most of these are known from single specimens only.” More recent estimates of the number of species of *Phinaea* have ranged from ca. six (Skog 1979) to 16+ (Burt & Wiehler 1995, Wiehler 2002c).

Fritsch (1893–1894) classified *Niphaea* and *Phinaea* with the Caribbean genus *Bellonia* L. in tribe Bellonieae. Species of all three genera have rotate to subrotate white corollas that are thought to have converged on a vibrational or “buzz” pollination syndrome (Wiehler 2002b). The genera of Bellonieae were included in an expanded tribe Gloxinieae by Wiehler (1983), although not necessarily as close relatives (Wiehler omitted any descriptions or discussions of these genera). This position, however, was not supported by Xu and Skog (1990), who continued to consider these three genera in the Bellonieae. Recent molecular analyses (Smith et al. 2004, Roalson et al. 2005a, Roalson et al. 2008) suggest that *Bellonia* is better placed in tribe Gesnerieae, but *Niphaea* and *Phinaea* are best placed in tribe Gloxinieae. Further, the segre-

* Corresponding author.

TABLE 1. Characters distinguishing the three genera, *Niphaea*, *Phinaea*, and *Amalophyllon*.

Character	<i>Niphaea</i>	<i>Phinaea</i>	<i>Amalophyllon</i>
Number of species	4	3-4	13+
Distribution	Central America	Central America, South America, West Indies	Central America, South America
Chromosome no.	$N = 11$	$N = 13$	$N = 13, 26$
Petiolation	distinctly petiolate	distinctly petiolate to subsessile	distinctly petiolate to subsessile
Leaf pairs	(sub)equal	(sub)equal	subequal to unequal
Leaf shape	ovate to elliptic	ovate to elliptic	elliptic to lanceolate
Leaf veins (color)	never silvery	sometimes silvery	never silvery
Leaf veins (number)	(2-)5-7 pairs	4-6 pairs	(4-)6-10+ pairs
Corolla symmetry	rotate to subrotate	subrotate to slightly zygomorphic	rotate to subrotate
Corolla color	white	white	white or (rarely) pink
Nectary	absent	annular	absent
Stamen filament length	shorter than anthers	longer than anthers	longer than anthers
Stamen filament curvature	not curved	curved	curved
Anther (thecae) shape	oblong	subglobose	subglobose
Anther thecae divergence	parallel	divergent	divergent
Ovary position	half inferior	half inferior	half inferior to almost superior
Pedicel posture	erect in fruit	erect in fruit	usually curved in fruit
Capsule apex	rostrate	not rostrate	not rostrate
Capsule texture (at dehiscence)	dry, lignified	fleshy, poorly lignified	dry, membranous
Valve dehiscence	opening slightly	spreading broadly	opening slightly
Valve trichomes	present	absent	absent
Seeds	falling freely	sticky, adhering to valves	falling freely

gation of *Niphaea* and *Phinaea* has been supported by molecular and morphological analyses (Zimmer et al. 2002, Smith et al. 2004, Roalson et al. 2005a), and these analyses do not support a close relationship between the two genera as suggested by some authors (Fritsch 1893-1894, Skog 1979).

One unexpected result of these analyses (particularly Roalson et al. 2005a, Roalson et al. 2008) is that two phylogenetically and morphologically distinct groups of species have been included in a polyphyletic *Phinaea*. Although both groups nest within Gloxinieae, these two groups are not closely related to each other, and neither group is closely related to *Niphaea*. The type species of *Phinaea*, *P. albolineata* (Hook.) Benth. ex Hemsl., belongs to a clade containing *Diastema* Benth., *Monopyle* Moritz ex Benth., and several species previously included in *Gloxinia* L'Hér. s.l. and later transferred to the genera *Gloxiniopsis* Roalson & Boggan, *Nomopyle* Roalson & Boggan, and *Gloxinella* (H.E.Moore) Roalson & Boggan (Roalson et al. 2005b). The other sampled species of *Phinaea* do not appear to have any close relatives within the tribe, at least as it has been sampled so far (Smith et al. 2004, Roalson et al. 2005a, Roalson et al.

2008). However, further molecular and morphological analyses (see below) have shown *Amalophyllon rupestre* Brandege, the type species of the monotypic genus *Amalophyllon* Brandege and originally described in Scrophulariaceae (Brandegee 1914), to belong to this group of *Phinaea* species. We have therefore applied that generic name to this group. *Niphaea* is closely related to neither *Phinaea* nor *Amalophyllon*; it is one of several Central American lineages in a polytomy at the base of the tribe with the Central American genera *Moussonia* Regel, *Achimenes* Pers., *Solenophora* Benth., *Eucodonia* Hanst., and *Smithiantha* Kuntze (Roalson et al. 2005a), or placed in a clade with the genera *Eucodonia*, *Moussonia*, and *Smithiantha* sister to the South American Gloxinieae clade (Zimmer et al. 2002, Roalson et al. 2008).

Species of *Niphaea*, *Phinaea*, and *Amalophyllon* are all small weak-stemmed herbs bearing scaly rhizomes and small white flowers with rotate to subrotate corollas. *Bellonia*, while similar in floral morphology, is a woody shrub and lacks scaly rhizomes. Although superficially similar, closer examination of *Niphaea*, *Phinaea*, and *Amalophyllon* has shown them to be distinct in several characters (TABLE 1). Species of all

three genera tend to be geographically restricted, widely separated from each other, and poorly collected. *Phinaea* has an especially interesting distribution: the three known species are widely disjunct (Mexico, Colombia/northern Brazil, W. Indies) although any mechanisms for long-distance dispersal are unknown; the fruits are similar to the “splash cup” fruits described for some *Gesneria* species (Skog 1976). In contrast, the genus *Niphaea* is restricted to Mexico and Guatemala. Species of *Amalophyllon* cover a wide geographic range in Central and South America and are discussed in more detail below. Following Bentham (1876), *Phinaea* has traditionally been separated from *Niphaea* on the basis of floral characters: *Niphaea* with anther cells oblong, parallel, locules confluent at the apices, and as long as or longer than the anther filaments and in *Phinaea* subglobose, divergent, with locules not confluent, and shorter than the filaments. While these characters do distinguish *Niphaea* from *Phinaea* and *Amalophyllon*, they do not distinguish *Phinaea* from *Amalophyllon*. In addition to these characters, we have found differences in fruit characters that distinguish all three genera from each other (TABLE 1).

Wiehler (1975, 1976a, 1976b, 1983) used artificial hybridization extensively as a tool to both test and shape generic circumscriptions in subfamily Gesnerioideae, but hybridization has not played a role in the classification of *Niphaea*,

Phinaea, and *Amalophyllon*. Intergeneric hybrids have been documented between *Niphaea* and *Achimenes* (Worley 1979, 1997, 2002; Wiehler 1983; Dates 1986) and between *Phinaea* and *Diastema* (Martens 1996). Purported hybrids between *Niphaea* and *Amalophyllon* (as *Phinaea*), *Niphaea* and *Eucodonia*, *Niphaea* and *Gloxinella* (as *Gloxinia*), and *Niphaea* and *Smithiantha* (Worley 1997, 2002) are not well documented. The nomenclature of nothogeneric taxa involving these genera has been discussed by Roalson and Boggan (2006).

The purposes of this paper are to (1) recognize *Amalophyllon* as a member of Gesneriaceae; (2) provide a complete generic description of *Amalophyllon*, in particular distinguishing it from the similar genera *Phinaea* and *Niphaea*; (3) transfer several species from *Phinaea* and *Niphaea* to *Amalophyllon*; (4) describe three new species: two in *Amalophyllon*, one in *Niphaea*; and (5) summarize the known species of all three genera, including a key to the genera and species.

We have described two new species in *Amalophyllon* for which we have adequate material, but there may be several additional undescribed species. A complete revision would be premature as most of these taxa are known only from single specimens or otherwise inadequate material. Unless otherwise noted, all types cited have been seen by the first and/or second author.

PRELIMINARY KEY TO THE SPECIES OF AMALOPHYLLON, NIPHAEA, AND PHINAEA

The following key will help separate the genera *Phinaea*, *Amalophyllon*, and *Niphaea*. The key to species is tentative, as the circumscriptions and geographic distributions of several species remain unclear and there are several undescribed species. Because many of the species of *Amalophyllon* are poorly known or collected, the species circumscriptions used for the key are largely based on geographic distributions supplemented by morphological characters.

- 1a. Filaments straight, usually equal to or shorter than anthers; fruit a dry rostrate capsule; valve trichomes present; plants of Mexico and Guatemala *Niphaea*
- 2a. Leaf blade less than 4 cm long with 2–5 pairs of veins; filaments longer than anthers; plants of Sinaloa, Mexico *N. pumila*
- 2b. Leaf blade more than 4 cm long with 5–7 pairs of veins; filaments equal to or shorter than anthers
- 3a. Corolla limb less than 2 cm in diameter; plants of Guerrero, México, and Oaxaca, Mexico *N. mexicana*
- 3b. Corolla limb 2 cm or more in diameter
- 4a. Leaf base acute to rounded, margins crenate to serrate; plants of Sinaloa, Mexico *N. sp. A*
- 4b. Leaf base cordate, margins serrate; plants of Guatemala and Chiapas, Mexico *N. oblonga*
- 1b. Filaments curved, longer than anthers; fruit a subglobose dry or fleshy capsule, never rostrate, valve trichomes absent; plants of Mexico, Central America, South America, West Indies
- 5a. Leaves sometimes with white or silver veins; nectary annular; fruit a fleshy capsule, valves opening to 180°, held on erect pedicel above leaves; plants of Central America, South America, and West Indies *Phinaea*
- 6a. Corolla with a distinct tube; lobes toothed; plants of South America *P. albolineata*
- 6b. Corolla tube nearly lacking; lobes entire; plants of Mexico, Central America, and West Indies
- 7a. Leaf margin serrate, apex acute; plants of southern Mexico *P. multiflora*

- 7b. Leaf margin crenate-serrate, apex obtuse; plants of the West Indies (Cuba, Haiti) *P. pulchella*
- 5b. Leaves never with white or silver veins; nectary absent; fruit a dry capsule, valves opening only slightly, often held on pedicel curving below leaves; plants of Mexico, Central America and South America *Amalophyllon*
- 8a. Plants of Central America
- 9a. Leaf blade 10–15+ cm long with 10 or more pairs of veins; flowers ca. 2 cm in diameter, white tinged pink; plants of Honduras *A. macrophyllodes*
- 9b. Leaf blade 3–13 cm long with fewer than 10 pairs of veins; flowers less than 2 cm in diameter, white, or if not white, less than 1 cm in diameter
- 10a. Leaf margin deeply double-serrate to lacerate/incised; flowers 1 cm or more in diameter; plants of Costa Rica and Panama *A. laceratum*
- 10b. Leaf margin crenate to serrate or dentate; flowers usually 1 cm or less in diameter (if larger, then leaves not deeply incised)
- 11a. Plants caulescent; leaves not congested, internodes and petioles at least 1 cm long; plants of Guatemala (?) *A. parviflorum*
- 11b. Plant subcaulescent or with the leaves congested at the ends of short stems; leaves subsessile to short-petiolate, petioles usually less than 1 cm long
- 12a. Leaf veins distinctly marked with purple; flowers pink; plants of Panama *A. sp. A*
- 12b. Leaf veins green or marked with purple; flowers white
- 13a. Leaves subsessile, blade elliptic to lanceolate, margins serrate, largest leaves with 7–10 pairs of veins; plants of Guatemala (Alta Verapaz) *A. repens*
- 13b. Leaves subsessile to petiolate, blade ovate to elliptic, margins crenate to serrate, largest leaves with 4–6 (–7) pairs of veins; plants of Mexico, Belize, Guatemala, El Salvador, Nicaragua, and Honduras *A. rupestre*
- 8b. Plants of South America
- 14a. Plants of Colombia and Venezuela
- 15a. Leaf blade longer than 8 cm, with 10 or more pairs of veins; plants of Antioquia, Colombia *A. macrophyllum*
- 15b. Leaf blade shorter than 8 cm, with fewer than 10 pairs of veins
- 16a. Flowers ca. 2 cm in diameter; plants of Colombia
- 17a. Petioles shorter than 1 cm; leaves ovate-lanceolate, margins coarsely dentate-serrate, leaf base rounded *A. albiflorum*
- 17b. Petioles longer than 1 cm; leaves ovate to elliptic, margins crenate to dentate, leaf base subcordate *A. rubidum*
- 16b. Flowers less than 1.5 cm in diameter; plants of Venezuela
- 18a. Leaf margins crenate *A. roezlii*
- 18b. Leaf margins biserrate *A. caripense*
- 14b. Plants of Ecuador and Peru
- 19a. Leaves ovate to elliptic, margins crenate to dentate, with 5–6 (–7) pairs of veins; corolla larger than 1 cm in diameter; plants of Ecuador and Peru *A. divaricatum*
- 19b. Leaves elliptic to lanceolate, margins deeply serrate to biserrate, with 7–8 (–10) pairs of veins; corolla smaller than 1 cm in diameter; plants of Ecuador *A. clarkii*

TAXONOMIC TREATMENT

Amalophyllon

Amalophyllon Brandegee, Univ. Calif. Publ. Bot. 6(4): 63. 1914. TYPE: *Amalophyllon rupestre* Brandegee.

Plants terrestrial or epipetric subcaulescent to caulescent herbs from scaly rhizomes; minutely puberulous, pilose, strigose, strigillose, sometimes glandular-pubescent; stems erect or decumbent, usually unbranched. **Leaves** opposite, subequal to unequal, frequently congested at the tops of the stems, subsessile to short-petiolate, rarely long-petiolate; blade membranous (papery and fragile when dry), elliptic, oblong, ovate, or

lanceolate, with (4–)6–10(–17) pairs of veins, margins crenate, dentate, serrate, biserrate, or lacerate, color green, purplish, or brownish (sometimes with dark markings), leaf bases cuneate to decurrent, rarely rounded to cordate, frequently unequal or oblique, apex acute to acuminate. **Inflorescences** axillary, epedunculate or rarely with a short peduncle, with minute bracteoles or ebracteolate, with (1–) 4+ flowers congested in the axil; pedicels long, slender, frequently curving below leaves in fruit; calyx 5-lobed, lobes elliptic to lanceolate; corolla 5-lobed, erect in the calyx, rotate to subrotate with a very short tube, white or rarely tinged pink, lobes entire, often with a fringe of glandular trichomes; fertile stamens 4 with a fifth reduced to

a minute staminode, inserted at the base of the corolla, filaments curved, anthers coherent or free, shorter than the filaments, thecae oblong-ovate to subglobose, divergent, dehiscing by a short slit or pore; nectary absent; ovary half-inferior to nearly superior, ovoid to subglobose; style slender, curved, longer than the stamen filaments; stigma capitate to stomatomorphic, rarely bilobed. **Fruit** a subglobose to ovoid dry bivalved loculicidal membranous capsule, lacking trichomes on the internal margins, opening slightly at dehiscence; seeds numerous, minute, ca. 0.3–0.4 mm, fusiform to subglobose, spirally striate, falling freely from the capsule. **Chromosome numbers** $N = 13, 26$.

Distribution and ecology. Central America (southern Mexico to Panama) and South America (Andes from the eastern range of Venezuela to central Peru) in colonies on shaded wet rocks or cliffs in forests, frequently near streams, rivers, or waterfalls or at the mouths of caves.

Comments. *Amalophyllon* Brandege, originally described in Scrophulariaceae and until now known only from the type collection from Chiapas, Mexico, was excluded from Scrophulariaceae and referred to Gesneriaceae as a synonym of *Achimenes* by Fischer (2004). Examination of the type of *Amalophyllon rupestre* Brandege shows that this taxon indeed belongs in Gesneriaceae but with a group of species previously included in *Niphaea* and *Phinaea*. The brief description, poor type material, and its misplacement in Scrophulariaceae have previously hindered the recognition of this taxon, but better material from near the type locality in Chiapas confirms its placement in Gesneriaceae. Although a 4-valved capsule was described as one of the generic characters, an isotype of *A. rupestre* at US has a bivalved loculicidal capsule, as is typical for most Gesneriaceae; “dehiscence” into four valves is likely an artifact of pressing. It is still unclear why Brandege placed this genus in Scrophulariaceae, as 4-valved capsules are not typical for that family and other characters are more consistent with Gesneriaceae. Although not explicitly described, the unilocular (rather than bilocular) ovary and parietal (rather than axile) placentation evident on the fruiting isotypes are among the characters traditionally used to distinguish Gesneriaceae from Scrophulariaceae. The generic name refers to the thin texture of the leaves, which are very fragile upon pressing (a characteristic of most species in this genus, but also *Phinaea* and *Niphaea*).

Amalophyllon differs from *Phinaea* primarily by fruit characters but several other characters can help distinguish these genera (TABLE 1). Leaves of *Amalophyllon* sometimes have a purplish coloration or markings, but never have sil-

very veins as sometimes found in *Phinaea* s.s. Additionally, an annular nectary is absent in *Amalophyllon*; the nectary is usually described as absent in *Phinaea* species (apparently in part on the basis of taxa now included in *Amalophyllon*) but dissections of fresh material of two members of *Phinaea* s.s., *P. albolineata* and *P. multiflora* C.V. Morton, revealed a weakly developed annular nectary in both (Boggan pers. obs.). The most striking differences distinguishing *Amalophyllon* from *Phinaea* s.s. are characteristics of the fruit. *Phinaea* fruits are held erect above the foliage and are fleshy at dehiscence, with the valves splitting broadly (to 180 degrees) and the sticky seeds adhering to them. The fruit of *Amalophyllon* is held on a slender curving pedicel, often below the leaves; the membranous capsule opens only slightly, the seeds falling freely from it saltshaker-style.

Amalophyllon is distinguished from *Niphaea* by a number of characters including floral and fruit characters and chromosome number (TABLE 1). Chromosome counts reported for *Amalophyllon* are $N = 13$ for *A. divaricatum* (Poepp.) Boggan, L.E.Skog, & Roalson (R.E. Lee, unpublished annotation on *Seacord CC 188b* at BH) and $N = 26$ for *A. repens* (Donn. Sm.) Boggan, L.E.Skog, & Roalson (Lee 1966, as *Phinaea repens* (Donn. Sm.) Soler.) whereas that of *Niphaea oblonga* is $N = 11$ (Lee 1964). Lee did not cite voucher specimens for his chromosome count of *Phinaea repens* and no specimens from BH are annotated with this information; the only voucher specimen from material cultivated at BH as *Phinaea repens* (Moore 8196 bis, originally from Escuintla, Guatemala) is *A. rupestre*. The only known chromosome count for *Phinaea* s.s. is for *P. multiflora*, $N = 13$ (Lee & Gear 1963).

Amalophyllon has a wide distribution ranging from southern Mexico through Central America to Venezuela, Colombia, Ecuador, and northern Peru. Twelve described species are recognized here, most with very restricted distributions. The plants grow in colonies in constantly moist, shaded habitats, usually on rocks or cliffs and frequently at the mouths of caves (Milewski 1987, Myhr 2007).

Species circumscriptions have proven to be difficult as several species appear to be extremely variable as evidenced by comparing duplicates of collections made from the same population, and from observations of cultivated plants. We have taken a broad circumscription of several of the species (e.g., *A. divaricatum*, *A. rupestre*, and *A. laceratum* (C.V.Morton) Boggan, L.E.Skog, & Roalson), but the circumscriptions and synonymy of these and other species require critical reexamination. Also, there are several apparently undescribed species of

which we still have inadequate material. Few, if any, of the taxa overlap in geographic distribution but the distributions and circumscriptions of most of the taxa, and the total number of species, are problematic. More collections, particularly of several poorly known Colombian and Venezuelan taxa, are needed for a complete revision of the genus.

Molecular and morphological analyses (Roalson et al. 2005b, Roalson et al. 2008) place *Amalophyllon* (as *Phinaea p.p.*) firmly within tribe Gloxinieae but do not suggest any close relatives; the association of *Amalophyllon* (as *Phinaea p.p.*) with *Heppiella* Regel (Roalson 2005a) has little support. While previous analyses (Roalson et al. 2005a, Roalson et al. 2008) have not included the type species of *Amalophyllon*, preliminary analyses of nrDNA ITS data (Roalson unpubl. data) strongly place *A. rupestre* in a clade with *P. divaricata* (*A. divaricatum*) and *P. sp. nov.* [USBRG 962-336] (here described as *A. clarkii* Boggan & L.E.Skog), suggesting that *Amalophyllon* is the correct name to apply to this taxon.

Amalophyllon albiflorum (Rusby) J.K.Boggan, L.E.Skog, & E.H.Roalson, comb. nov. BASIONYM: *Phinaea albiflora* Rusby, Descr. S. Amer. Pl.: 124. 1920. TYPE: Colombia—Magdalena: “Santa Marta”, Sierra de Onaca, 4000–5000 ft, Aug 22 [1898 or 1899], *H.H.Smith 2506* (Holotype: NY).

Distribution and ecology. Colombia (Magdalena), collected on wet rocks at 1200–1500 m.

Comments. Duplicates of *H.H.Smith 2506* at CM, GH, and US were cited as isotypes by Ayers and Boufford (1988). There are duplicates of *Smith 2506* at several herbaria, but it is not clear which, if any, duplicates bearing this number other than the holotype itself can be considered type material. Other than the holotype, none of the duplicates we have seen bears complete label data and H.H. Smith collections sometimes include specimens collected at different localities or on different days under the same collection number (Ayers & Boufford 1988).

A collection from Chiriquí, Panama, cited as *Phinaea albiflora* in the Flora of Panama (Skog 1979), is not *A. albiflorum* and may be referable to *A. rupestre* (q.v.).

Material included in previous molecular analyses (Smith & Atkinson 1998, Smith et al. 2004) as “*Phinaea albiflora*,” sampled from a living accession at the Smithsonian Institution (USBRG 94–503), was in fact *Phinaea multiflora* (Boggan pers. obs.).

Representative specimens. Colombia—Magdalena: Mount San Lorenzo, near Santa Marta,

1900–2400 m, Jul 1932, *Seifrizz 160* (US); Santa Marta, *H.H.Smith 2506* (CM, F, L, US); along road from Santa Marta via Minca, El Campano and Telecom Station to top of Cerro Ramo, 1400 m, 19 Aug 1993, *Wiehler 93256* (SEL, US).

Amalophyllon caripense (Klotzsch & Hanst.) J.K.Boggan, L.E.Skog, & E.H.Roalson. BASIONYM: *Niphaea caripensis* Klotzsch & Hanst., Linnaea 27: 704, 730. 1856. TYPE: Venezuela, Monagas: “an den Felsen vor der Höhle Buacharo bei Caripe,” *Moritz 409*, Jul-Aug 1843 (Holotype: B (destroyed)). *Phinaea caripensis* (Klotzsch & Hanst.) Benth. & Hook.f. ex Soler., Beih. Bot. Centralbl. 34: 436. 1909.

Distribution and ecology. Venezuela (Monagas), at cave mouths.

Comments. *Amalophyllon caripense* is the easternmost species of the genus, occurs far outside the range of any other species, and is known only from the type. We are unable to designate a lectotype or neotype as we have not seen any specimens or found any duplicates of the type, although some may be extant; a possible duplicate at BM could not be found (Vicker pers. comm.). However, the description of the plant as having subsessile leaves with doubly serrate margins and small flowers of ca. 1.25 cm in diameter, and in particular its discovery at the mouth of a cave, is consistent with *Amalophyllon*.

Amalophyllon clarkii J.K.Boggan & L.E.Skog, sp. nov. TYPE: Ecuador, Azuay: Cuenca, Bosque Protector Molleturo Mullopungo, 250–300 m, 12 Apr 1996, *J.L. Clark et al. 2490* (Holotype: QCNE; Isotypes: COL, SEL, SRP, US). FIGURE 1.

Herbaceum pusillum ecuadorensis in corollis albis ad *A. divaricatum* simile sed in foliis profundius serratis et in corollis minus quam 1 cm in diametro differt.

Plant a diminutive epipetric herb from scaly rhizomes; stem short, erect to ascending, 0–1 (–4) cm long, unbranched. **Leaves** opposite, subequal, subsessile to short-petiolate, petioles 0.5–1 cm long, strigose, blade membranous, papery and fragile when dry, slightly bullate, elliptic to lanceolate, 2–6 (–10) cm long, 1–2 (–3) cm wide, with 7–8 (–10) pairs of veins, margins deeply serrate or biserrate, bright green, usually with purplish veins, base cuneate to decurrent, apex acute, strigillose above and below, strigose on the veins beneath. **Inflorescences** axillary, ependunculate, ebracteolate, with 1–4 (–12) flowers per axil; pedicels slender, curved, 2–3 cm long, strigose; calyx lobes 5, subequal, linear-lanceolate, free at the base, with 0–2 teeth distally, ca.

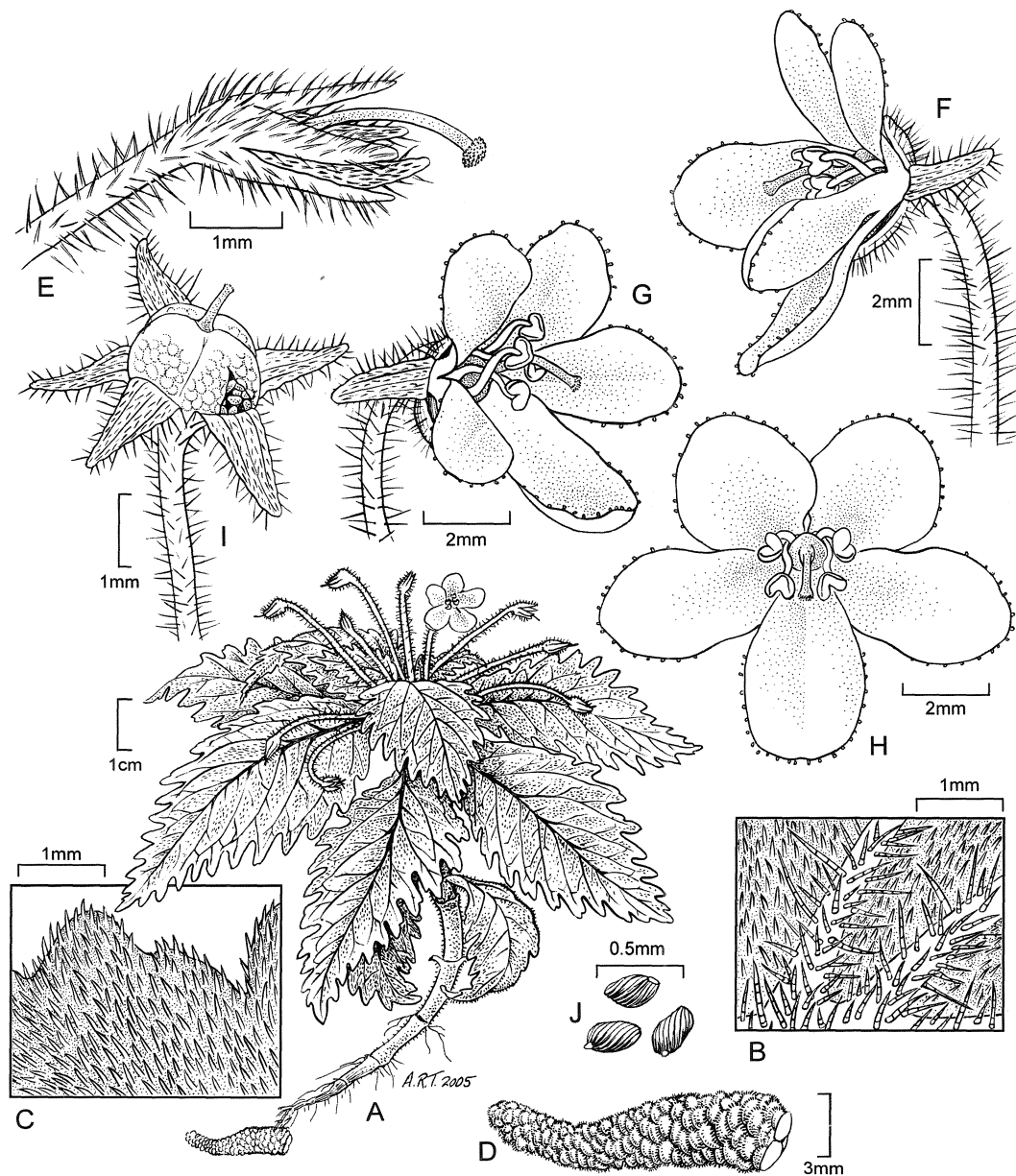


FIGURE 1. *Amalophyllon clarkii*. A. Habit. B. Section of lower leaf surface. C. Section of upper leaf surface and margin. D. Rhizome. E. Lateral view of flower with corolla removed. F. Lateral view of flower. G. Lateral view of flower showing stamens and pistil. H. Face view of flower. I. Mature fruit. J. Seeds. A–J: drawn from live material (accession # USBRG 96-336), voucher J.L. Clark et al. 2490 (US).

2 mm long, strigose; corolla 5 (–6)-lobed, erect in the calyx, subrotate, white, limb ca. 8 mm across, lobes entire, subequal, spreading broadly at anthesis, slightly united at the base to form a very short tube, apices rounded, upper 2 lobes broadly ovate, ca. 2 mm long x 2 mm wide, lower 3 lobes oblong, ca. 3 mm long, 2 mm

wide, glabrous inside, outside with a few sparse hairs, margin with a fringe of glandular hairs; fertile stamens 4 (–5), inserted at the base of the corolla, filaments yellow, ca. 2 mm long, anthers yellow, free, thecae oblong-ovoid, strongly divergent, ca. 0.5 mm long, glabrous; dorsal stamens minute, sterile, ca. 0.5 mm long; nectary

absent; ovary almost fully superior, subglobose, glabrous, ca. 1 mm long and wide, style ca. 2 mm long, curved, glabrous, stigma capitate. **Fruit** a subglobose, dry, bivalved, membranous capsule 1.5–2 mm in diameter, loculicidally dehiscent, valves opening slightly, lacking a fringe of trichomes on the internal margins of the valves; seeds ca. 0.3 mm long, elliptic, brown, spirally striate.

Phenology. Flowering in March, April, June, and July; in cultivation flowering almost continuously.

Distribution and ecology. Ecuador, known from the provinces of Azuay, Esmeraldas, Guayas, and Los Ríos, collected in wet forest on rocks at 120–300 m.

Comments. *Amalophyllon clarkii* is easily distinguished from *A. divaricatum*, the only other species known to occur in Ecuador, in having subsessile leaves that are smaller, narrower, more deeply serrate, and in having smaller flowers. In cultivation the tiny flowers are ephemeral and each is open for only a few hours in the morning, usually falling by midday.

Living material of *Clark 2490* was cultivated at the Smithsonian Institution under the accession number USBRG 96-336 and has been included in recent phylogenetic studies (Roalson et al. 2005a, Roalson et al. 2008) as "*Phinaea* sp. nov. [96-336]." In cultivation the plant is quite variable in vegetative characters such as leaf size, shape, and coloration. This morphological variation even within a single clone due to cultural conditions (similarly noted in cultivated material of *A. rupestre*, q.v.) suggests caution in describing and circumscribing other species. The specific epithet honors John L. Clark, whose collection brought this undescribed species to our attention.

A specimen collected in Esmeraldas (*Hirtz 3629*), annotated by Wiehler with the unpublished name "*Phinaea hirtzii* Wiehler, sp. nov.," appears to belong to this species but occurs at some distance from the other collections. "*Phinaea hirtzii* Wiehler ined." was also cited (Wiehler 2002c) from Cotopaxi, Ecuador, but we have not seen any collections of *Phinaea* or *Amalophyllon* from this region by Hirtz or by any other collector.

Paratypes. Ecuador—Azuay: Cuenca, Bosque Protector Molleturo Mullopungo, 250–300 m, *J.L. Clark et al. 2490*, cultivated at the Smithsonian Institution as USBRG 96-336, 22 Jul 2002, *Skog & Boggan 8225* (US); Esmeraldas: area of Lita and Alto Tambo, Estero Hondo, 15 Jun 1988, *Hirtz 3629* (SEL); Guayas: Tere-sita, 3 km W of Bucay, 270 m, 5–7 Jul 1923,

Hitchcock 20550 (GH, NY, US); Los Ríos: Hcda. Clementina, hacia hito 1, 120 m, 21 Mar 1996, *Cornejo & Bonifaz 4830* (SEL, US); Hacienda Clementina, E slope of Cerro Samama, ca. 38 km NE of Babahoyo, 200–300 m, 21 May 1994, *Ståhl & Knudsen 1152* (S); Hacienda Clementina, Cerro Samama, near Puerto Negra, 200–250 m, 23 May 2002, *Ståhl & Cornejo 5854* (S, US).

Amalophyllon divaricatum (Poepp.) J.K.Boggan, L.E.Skog, & E.H.Roalson, comb. nov. BASIONYM: *Trevirana divaricata* Poepp., Nov. Gen. Sp. Pl. 3: 9. 1840. TYPE: Peru—Huánuco: Cassapi, Jan 1830, *Poeppig 1629* (Holotype: W). *Diastema divaricatum* (Poepp.) Benth. ex Walp., Repert. Bot. Syst. 6: 403. 1847. *Phinaea divaricata* (Poepp.) Wiehler, Selbyana 5: 64. 1978.

Phinaea ecuadorana Wiehler, Gesneriana 1: 84, fig. 28. 1995. TYPE: Ecuador, El Oro: along road from Loja to Santa Rosa, 20 km past Piñas, 17 Apr 1986, *H. Wiehler & GRF Expedition 8652* (Holotype: QCNE; Isotypes: B, E, K, MO, NY, QCA, SEL, US).

Distribution and ecology. Southern Ecuador (El Oro, Loja) and Peru (Huánuco, Junín, San Martín, Ucayalí), on wet rocks or cliffs, frequently at the mouths of caves, at 280–950 (–1900?) m.

Comments. Duplicates of *Poeppig 1629* are extant at several herbaria but at least some of these specimens are not part of the type collection, so we have not cited any of them as isotypes.

We have taken a broad circumscription of this species and further study may prove that some collections represent distinct taxa. The type and most collections are from Huánuco, Peru, but even within this area collections exhibit considerable variation. The type of *Phinaea ecuadorana* Wiehler falls within this range of variation, but comes from Ecuador at some distance from other collections; further study may show it merits recognition as a valid species. A collection from Junín, Peru (*Woytkowski 35360*) is less isolated from other populations of this species but was collected at 1900 m, a much higher altitude than any other collection.

Representative specimens. Ecuador—Loja: Bosque Petrificado Puyango, quebrada Quemazones, 280 m, 17 Apr 1996, *Cornejo & Bonifaz 5051* (US). Peru—Huánuco: along road from Tingo Maria to Monson, vicinity of Río Patay Rondos, Cuevas de Gucharo "Parque Nacional Tingo Maria," 650 m, 4 Apr 1984, *Croat 57934, 57939* (MO, US); Leoncio Prado, Tingo Maria, Cueva de Los Lechusas, Valley of Río Monzon, 680 m, 9 Aug

1980, *Gentry & Salazar* 29535 (MO); on road between Last Palmas and Cayumba, 26.5 km from Tingo Maria on road to Huánuco, 1 Jun 1960, *Moore et al.* 8548 (BH, SEL, USM); Cuchero, 1829, *Poeppig* 1629 (OXF, W); Prov. Leoncio Prado. Dtto. Rupa Rupa, en el interior de la Cueva de las Lechuzas, 670 m, 4 Jun 1969, *Schunke* V. 3103 (F, US), 3104 (COL, F, NY, US); near Tingo Maria, on road to Las Palmas, 26.4 km from Tingo Maria, *H.E. Moore* 8548A, grown in the Hortorium Conservatory, Cornell Univ., Ithaca, as G-491, 27 Jun 1968, *Seacord* CC 188b (BH); Junín: Prov. Tarma, Utcuyacu, 1900 m, 19 Feb 1948, *Woytkowski* 35360 (F, MO, UC, USM); San Martín: Rioja, Agua Verdes, 900 m, 2 Apr 2001, *van der Werff et al.* 16604 (US); Prov. Rioja, Carretera Rioja-Pedro Ruiz, caves of Aguas Verdes, 950 m, 24 Mar 1998, *van der Werff et al.* 15590 (US); Ucayali: Prov. Coronel Portillo, Cordillera Azul, km 15 on Tingo Maria-Pucallpa road, 1 km on dirt road that begins at Puente Pumahuasi, 700 m, 5 Jun 1981, *Young & Sullivan* 733 (MO, US). Origin unknown: Cultivated in the Smithsonian greenhouses as USBRG 98-008, 17 May 2000, *Skog & Boggan* 8039 (US).

Amalophyllon laceratum (C.V.Morton) J.K.Boggan, L.E.Skog, & E.H.Roalson, comb. nov. BASIONYM: *Phinaea lacerata* C.V.Morton, Ann. Missouri Bot. Gard. 24: 203. 1937. TYPE: Panama, Chiriquí: Río Chiriquí Viejo valley, vicinity of Monte Lirio, 1300–1900 m, 27 Jun–13 Jul 1935, *R.J. Seibert* 316 (Holotype: MO; Isotype: US).

Distribution and ecology. Costa Rica (Alajuela, Puntarenas) and Panama (Bocas del Toro, Chiriquí, Veraguas), on wet rocks and cliffs along streams or rivers at (250–) 1000–2100 m.

Comments. The deeply incised/lacerate leaves distinguish this species from all others, but this character appears to be somewhat variable, particularly in specimens from lower elevations. One such collection from Bocas del Toro, Panama (*D'Arcy* 16383) has larger and less deeply incised leaves than other collections of this species and may represent a new species.

Representative specimens. Costa Rica—Alajuela: Río Jesús de San Ramón, 8500 ft, Sep 1921, *Brenes* 3547, 3548a (F); Guadalupe de Zarco, Canton Alfaro Ruiz, 1550 m, 1 Jul 1938, *A. Smith* NY807 (F, NY); Puntarenas: Cantón de Buenos Aires, Cuenca Térraba-Sierpe, Estacion Tres Colinas, Finca Benito Acuna, 1700 m, 10 Sep 1996, *Alfaro* 747 (INB, MO); along Río Coto Brus, near Cotan, 23 km north of La Unión (on Panama border), 9 Aug 1974, *Croat* 26676 (MO, US); foothills of the Cordil-

lera de Talamanca, along the Río Bella Vista, NW of Las Alturas, 1450–1600 m, 30 Aug 1983, *Davidse* 24309 (MO, US); Cantón de Buenos Aires Ujarrás, cabeceras de Río Kuyé, siguiendo las Filas que dan a Olán, 1450 m, 20 Sep 1989, *Herrera* 3512 (US); Coto Brus, Reserva de la Biosfera de la Amistad, cerca Estación Biológica Las Alturas de Coton, 1455–2100 m, 8 Jul 1994, *Kress & Runk* 94-4661 (US); Cantón de Coto Brus, Cuenca Térraba-Sierpe, Las Mellizas, Finca Santa Marta, 1500 m, 15 Sep 1996, *Navarro* 440 (INB, US). Panama—Bocas del Toro: Valle del Silencio, 6000 ft, 8–10 Aug 1979, *Antonio* 1681 (MO, US); east 1.5 mi off road from divide to Chiriquí Grande, 250–300 m, 24 Jun 1986, *D'Arcy* 16383 (MO); Chiriquí: west of Cerro Pando, 6000 ft, 9 Aug 1972, *D'Arcy & D'Arcy* 6641 (MO, PMA, US); Camp Hornitos (Fortuna dam site), 1000 m, 23 Sep 1976, *Dressler* 5437 (PMA, SEL); Fortuna dam site, 1400–1600 m, 15 Sep 1977, *Folsom et al.* 5609 (MO, US); valley of the upper Río Chiriquí Viejo, 1300–1900 m, Jul–Aug 1937, *White & White* 29 (GH, MO, US).

Amalophyllon macrophyloides J.K.Boggan & L.E.Skog, sp. nov. TYPE: Honduras—Yoro: foothills of the Cordillera Nombre de Dios, S of San José de Texíguat and on the western side of the canyon of the Río Texíguat, 250–250 m, 15 May 1991, *G. Davidse et al.* 34402 (Holotype: US; Isotype: MO).

FIGURE 2.

Herbaceum hondurense ad *A. macrophyllum* simile sed in limbis corollarum roseis et majoribus ca. 2 cm in diametro distinctum.

Plant a subcaulescent epipetric herb from scaly rhizomes, stem erect to ascending, 1–2 cm long, unbranched, with leaves congested at the tips, pilose. **Leaves** opposite, subequal to unequal, sessile, petioles 0.2–0.3 cm long, villous, blade membranous, papery and fragile when dry, elliptic to narrowly obovate or lanceolate, sometimes falcate, 10–15 (–20) cm long, 3–5 (–6) cm wide, with (7–) 10–15 (–20) pairs of veins, margins dentate to serrate, base rounded to decurrent, frequently unequal and oblique, apex acute, sparsely strigose above, sparsely strigose on the veins below. **Inflorescences** axillary, pedunculate, ebracteolate, with 2–4+ flowers congested in the axil; pedicels slender, curved, 2–4 cm long, pilose; calyx lobes 5, subequal, lanceolate, ca. 2 mm long, ca. 1 mm wide, entire, apex acute, sparsely pilose inside and outside, slightly accrescent in fruit; corolla 5-lobed, erect in the calyx, limb subrotate, white tinged pink, 1.8–2 cm across, lobes entire, subequal, spreading broadly at anthesis, slightly united at the base to form a very short tube,

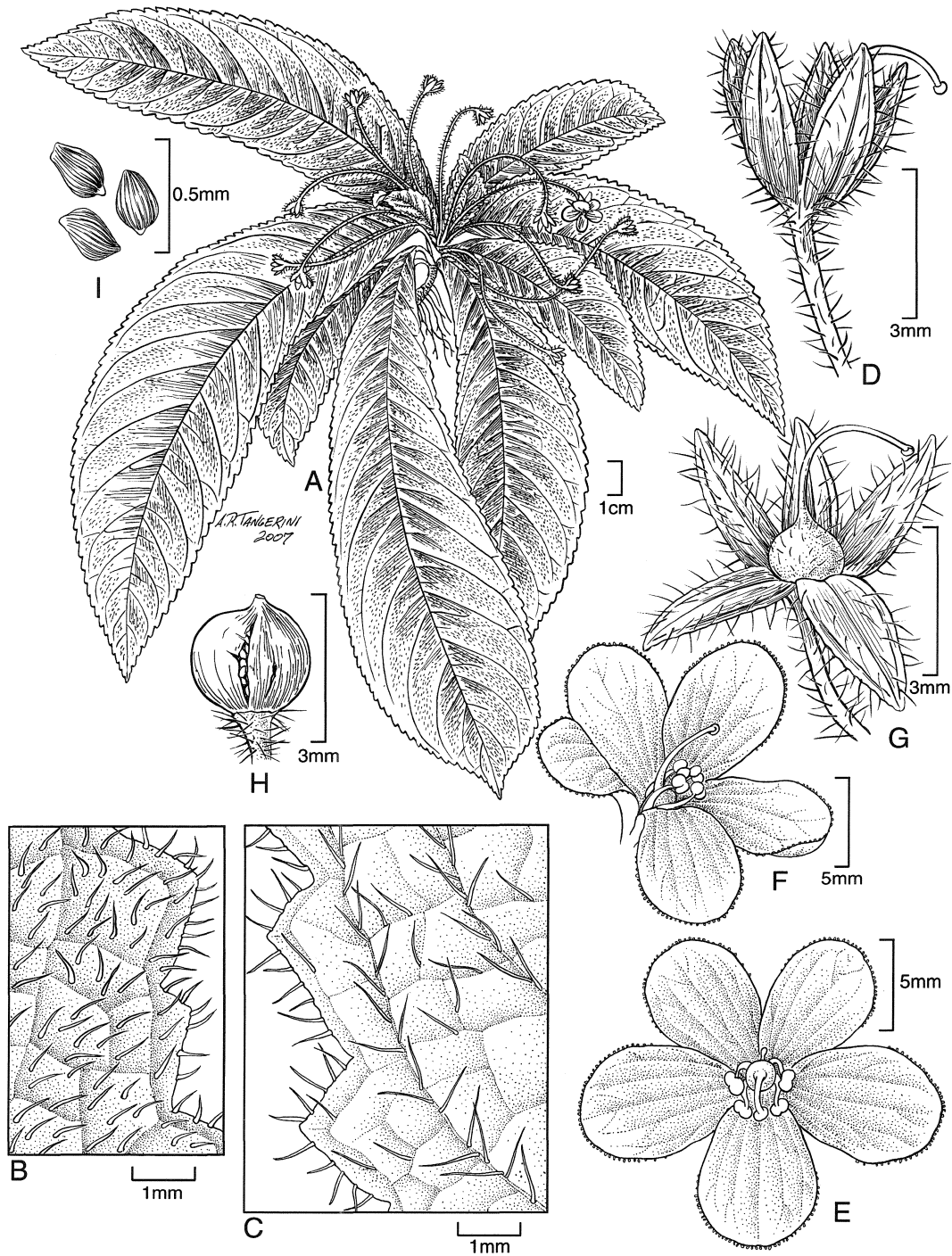


FIGURE 2. *Amalophyllon macrophyllodes*. A. Habit. B. Section of upper leaf surface and margin. C. Section of lower leaf surface and margin. D. Lateral view of flower with corolla removed. E. Face view of flower. F. Lateral view of flower with calyx removed showing corolla, stamens, and pistil. G. Lateral view of flower with corolla removed showing ovary. H. Mature fruit with calyx removed. I. Seeds. A: drawn from Hazlett *et al.* 8019 (MO). B–I: drawn from Davidse *et al.* 34402 (US).

apices rounded, upper 2 lobes obovate, ca. 6 mm long \times 5 mm wide, lower 3 lobes obovate, ca. 8 mm long \times 6 mm wide, glabrous inside and outside, margins entire with a fringe of glandular hairs; fertile stamens 4, inserted at the base of the corolla, filaments curved, ca. 2 mm long, anthers free, thecae subglobose, ca. 1 mm long, slightly divergent, glabrous; staminode not observed; nectary apparently absent; ovary nearly superior, subglobose, sparsely villous, ca. 1.5 mm in diameter, style ca. 3 mm long, curved, glabrous, stigma capitate. **Fruit** globose, ca. 2 mm in diameter; seeds ca. 0.3 mm long, rhomboid to ellipsoid, dark brown, spirally striate.

Phenology. Flowering and fruiting in April and May.

Distribution and ecology. Known only from the Yoro/Atlantida border area of Honduras in the vicinity of the Rio Texiguat, on rocks or cliffs near streams at 250–500 m elevation.

Comments. This taxon is distinct from all other Central American species of *Amalophyllum*; its unusually large leaves (to 20 cm long) suggest the Colombian species *A. macrophyllum* Wiehler, but that species has an indument of glandular trichomes, flowers that are smaller (ca. 1 cm in diameter) and white, and a glabrous ovary. Some collections of *A. laceratum* from Costa Rica and Panama (e.g., *Herrera 3512*, *D'Arcy 16383*) approach *A. macrophyloides* in leaf size, but have white flowers and are otherwise morphologically distinct. The specific epithet refers to the resemblance of this taxon to *A. macrophyllum*.

Paratype. Honduras—Atlantida: ravines E of Texiguat ("Texiguat") River, 1–2 km SW of aldea La Aurora, 9 April 1994, *Hazlett et al. 8019* (MO).

Amalophyllum macrophyllum (Wiehler) J.K.Boggan, L.E.Skog, & E.H.Roalson, comb. nov. BASIONYM: *Phinaea macrophylla* Wiehler, *Gesneriana* 1(1): 86, fig. 29. 1995. TYPE: Colombia, Antioquia: road Medellín-Bogotá, at Refugio Ecologico del Cañon del Río Claro, a tributary of Río Magdalena, 21 Nov 1986, *H.Wiehler & GRF Expedition 86299* (Holotype: HUA; Isotypes: COL, K, NY, SEL, US).

Distribution and ecology. Colombia (Antioquia), on rocks, cliffs and at cave mouths at 300–800 m.

Comments. Plants initially identified and illustrated as *Phinaea rubida* Lem. (Milewski 1987) were later described as a new species, *Phinaea macrophylla* Wiehler. *Amalophyllum*

macrophyllum is apparently endemic to Antioquia and, due to its unusually large leaves (to nearly 30 cm), is unlikely to be confused with any other South American taxon.

Representative specimens. Colombia—Antioquia: Mpio. San Luis, región Río Claro, Refugio 3h. S.E. Medellín, via Medellín-Bogotá, 800 m, 18 Feb 1987, *Callejas 3255* (NY); Mpio. de San Luis, cañon del río Claro, margen izquierda, sector occidental, 330–400 m, 1 Sep 1983, *Cogollo & Borja 644* (MO); along Río Claro, below San Luis, near Bogotá-Medellín highway, 300 m, 13 Sep 1982, *Folsom & Renteria 10345* (US); road Medellín-Bogotá, at Refugio Ecologico del Cañon del Río Claro, a tributary of Río Magdalena, 22 Mar 1987, *Wiehler et al. 8748* (SEL, US).

Amalophyllum parviflorum (A.Braun & Bouché) J.K.Boggan, L.E.Skog, & E.H.Roalson, comb. nov. BASIONYM: *Niphaea parviflora* A.Braun & Bouché, *Linnaea* 25: 299. 1853. *Phinaea parviflora* (A.Braun & Bouché) Benth. & Hook.f. ex Soler., *Beih. Bot. Centralbl.* 24(2): 436. 1909. *Niphaea warszewiczii* Hanst., nom. nud. pro syn., *Linnaea* 27: 75. 1856. TYPE: Guatemala. Described from plants cultivated at Berlin, of unknown origin in Guatemala originally collected by Warszewicz, Hort. bot. Berol., *Hanstein s.n.* (BR, lectotype designated here).

Distribution. Guatemala.

Comments. The precise type locality is unknown and the holotype, if any existed, was presumably at B and no longer extant. A specimen at BR that was made from cultivation in Berlin closely matches the original description and is almost certainly a duplicate of the original type material. We have therefore designated this specimen as the lectotype.

Niphaea parviflora is the oldest name that has been applied to any *Amalophyllum* species. We have not seen any specimens from Guatemala that precisely match the description or lectotype of *A. parviflorum* and cannot be certain that the original material actually came from Guatemala. The other species occurring in Guatemala, *A. repens* and *A. rupestre*, are morphologically distinct, although it is possible that all three taxa represent a single variable species to which the name *A. parviflorum* would then be applied. Recent collections from Belize (*Whiteford 1120*, *1206*, *Myhr RM2006-01*) as well as some from El Salvador (*Reyna 1451*, *Worth et al. 8848*) approach *A. parviflorum* in having a more caulescent and petiolate habit but have larger flowers than those described for *A. parviflorum*, and we have included these collections under *A. rupestre*.

tre. Until the type locality of *Niphaea parviflora* is more precisely determined and unambiguous wild collections can be examined and compared with other taxa, we maintain *A. parviflorum* separate from the other species.

Amalophyllon parviflorum is unusual in the genus for being distinctly caulescent with leaf pairs separated by long internodes. The specific epithet refers to the small flowers of this taxon with respect to those of the other *Niphaea* species known at the time of its description, *N. oblonga*, *N. rubida* (now *Amalophyllon rubidum*) and *N. albolineata* (now *Phinaea albolineata*) but similarly small flowers are typical for many species of *Amalophyllon*. In her treatment for the Flora of Guatemala, Gibson (1974) indicated that she did not see type material of this taxon and expressed misgivings about her circumscription of it; her description of *Phinaea parviflora* in the flora is probably based primarily on specimens of the similarly small-flowered *A. rupestre* (q.v.). The treatment of Gesneriaceae in Flora de Nicaragua (Skog 2001) similarly treated *A. rupestre* as *Phinaea parviflora*.

Amalophyllon repens (Donn. Sm.) J.K.Boggan, L.E.Skog, & E.H.Roalson, comb. nov. BASIONYM: *Napeanthus repens* Donn.Sm., Bot. Gaz. 31: 118. 1901. TYPE: Guatemala, Alta Verapaz: Cubilquitz, 350 m, Jul 1901, *H.von Tuerckheim* 7647 (Lectotype: designated here, US 1336666; Isolectotypes: GH, K, NY, M, US (2)). *Phinaea repens* (Donn.Sm.) Soler., Beih. Bot. Centralbl. 24(2): 435. 1909.

Distribution and ecology. Guatemala, on damp rocks at 350 m.

Comments. The protologue cites the type as *Tuerckheim* 7647, but of the two sheets of this collection at US received from the Donnell Smith herbarium, it is impossible to determine that either is the holotype. Furthermore, all duplicates of *Tuerckheim* 7647 that we have seen bear a collection date of July 1901, whereas the protologue cites a collection date of June 1900. Donnell Smith himself later (1903) cited the collection date for this collection as July 1901, suggesting that the protologue is in error.

As circumscribed here, *Amalophyllon repens* is restricted to the state of Alta Verapaz in Guatemala. Gibson's (1974) description of this species for the Flora of Guatemala is probably based on a mixture of this species and *Amalophyllon rupestre* (q.v.). The relationship between these two species is probably a close one and further study may prove them to be conspecific.

Representative specimens. Guatemala—Alta

Verapaz: Cubilquitz, 350 m, Jul–Aug 1907, *Tuerckheim* II 89 (F, GH, LY, MO, NY, US).

Amalophyllon roezlii (Regel) J.K.Boggan, L.E.Skog, & E.H.Roalson, comb. nov. BASIONYM: *Niphaea roezlii* Regel ("Roezli"), Gartenfl. 26: 67–68, pl. 896. 1877. *Phinaea roezlii* (Regel) Wiehler, nom. inval., The Gloxinian 52(3): 36. 2002. TYPE: Venezuela. Apparently described from plants cultivated from seeds collected by Roezl in Venezuela; no specimens seen, probably typified by the illustration.

Distribution. Venezuela. The exact locality of the type collection is unknown, but specimens tentatively identified as this species have been collected in the states of Mérida and Trujillo.

Representative specimens. Venezuela—Mérida: Pueblos del Sur, 1600–2200 m, Jun 1955, *Bernardi* 2307 (NY); Dto. Arzobispo Chacón, orillas de la carretera entre las poblaciones de Canaguá y Mucuchachí, 975–1500 m, 10 Aug 1970, *Ruiz-Teran & Lopez-Figueiras* 633 (US); Trujillo: Boconó, Parque Nacional Guaramacal, vertiente occidental, sector El Santuario, alrededores de La Cueva, 1800 m, 1 May 1999, *Cuello et al.* 1444 (PORT).

Amalophyllon rubidum (Lem.) J.K.Boggan, L.E.Skog, & E.H.Roalson, comb. nov. BASIONYM: *Niphaea rubida* Lem., Fl. Serres Jard. Eur. 3(7): 251, pl. 9. 1847. TYPE: described from cultivated material of unknown origin (probably Colombia); no specimens seen, probably typified by illustration. *Phinaea rubida* (Lem.) Fritsch, Nat. Pflanzenfam. 4(3b): 173, pl. 77A. 1894.

Niphaea crenata H.Karst., Fl. Columb. 1: 161–162, pl. 80 (1861). TYPE: Colombia, Norte de Santander: prope Ocaña, 1000 m. No specimens seen, probably described from cultivated plants and typified by the illustration.

Distribution and ecology. Colombia (Magdalena, Norte de Santander), collected at 1000–1380 m.

Comments. Fritsch (1893–1894, 1916) and Wiehler (2002c) treated *N. crenata* as a synonym of *Phinaea rubida*, but this synonymy should be critically re-examined. Although both taxa are described with excellent illustrations, we have not seen any type specimens. US has a photograph of a specimen at P made from cultivated material of *Niphaea rubida* in April 1850 (collector unknown) that is probably a clone-type.

The only other taxon of this group known from Norte de Santander is *Phinaea albolineata*,

with which *A. rubidum* cannot be easily confused. Although similar in general aspect to *Niphaea oblonga* and synonymized under that species by Beddome (1908), both the illustration and description of *Niphaea rubida* show the anthers to be subglobose in shape and shorter than the filaments.

Seeds illustrated under the name *Niphaea rubida* by Beaufort-Murphy (1983) came from a specimen determined by us to be *Phinaea multiflora* (Moore & Bunting 8696). Colombian plants discussed and illustrated as *P. rubida* (Milewski 1987) were later described as the new species *P. macrophylla* (now *Amalophyllon macrophyllum*).

Representative specimens. Colombia—Magdalena: Sierra Nevada de Santa Marta, southeastern slopes, Hoya del Río Donachuí, fields and roadsides around Donachuí, 1350–1380 m, 23 Sep 1959, Cuatrecasas & Castaneda 24363 (F, US)

Amalophyllon rupestre Brandegee, Univ. Calif. Publ. Bot. 6(4):63, 1914. TYPE: Mexico, Chiapas: Finca Irlanda, Sep. 1913, C.A. Purpus 7064 (Holotype: UC; Isotypes: GH, NY, US).

Napeanthus saxicola Brandegee, Univ. Calif. Publ. Bot. 6(4): 65, 1914. TYPE: Mexico, Chiapas: near Finca Covadonga, Sep. 1913, C.A. Purpus 6701 (Holotype: UC; Isotypes: F, GH, NY, US). *Niphaea saxicola* (Brandegee) D.N. Gibson, Phytologia 23: 337, 1972.

Distribution and ecology. Mexico (Oaxaca and Chiapas), Belize, Guatemala, El Salvador, Honduras, and Nicaragua, collected on wet rocks and cliffs along streams and at cave mouths at 150–1600 m.

Comments. It is remarkable that Brandegee (1914) described *Amalophyllon rupestre* as a new genus, and even in a different family (Scrophulariaceae) in the same paper in which he described *Napeanthus saxicola*. Both taxa were based on Purpus collections from localities very close to each other in Chiapas, Mexico, and their respective type collections are morphologically very similar and were collected in similar habitats (in fact, both specific epithets refer to dwelling on or among rocks). Their original descriptions are also very similar except for the 4-valved fruit described for *A. rupestre*, which is probably an artifact of pressing (see above). After studying numerous specimens, including several from near the type localities, we have concluded that the two taxa are conspecific. Because both names were published at the same time in the same publication, neither has nomenclatural

priority over the other. Neither name is well-established in the literature; we have chosen to take *A. rupestre* as the valid name, as this name represents the type species of the genus, the description and type collection of this taxon is more complete, and more closely matches the specimens we have seen.

Amalophyllon rupestre is a variable species that has been confused with several other taxa and, as broadly circumscribed here, may represent a complex of two or more closely related species. Gibson saw specimens of this taxon in the course of her studies for the Flora of Guatemala (Gibson 1974) but, probably because *Amalophyllon rupestre* had been described in Scrophulariaceae, did not associate any specimens with this name; she variously annotated specimens as *Niphaea saxicola*, *Phinaea repens*, and *Phinaea parviflora*. Her descriptions of the latter two taxa in the Flora of Guatemala reflect this confusion. As noted by Morales & Skog (unpubl. data), Gibson's (1972) transfer of *Napeanthus saxicola* Brandegee to *Niphaea* was erroneous; it is unclear why Gibson made this transfer as the characters she cited as supporting this placement ("subglobose anthers with distinct thecae not confluent at the apex") are the same characters she used (Gibson 1974) to distinguish *Phinaea* (s.l.) from *Niphaea*.

Amalophyllon rupestre has a scattered range from southern Mexico through southern Guatemala, Belize, El Salvador and Nicaragua and possibly as far south and east as Panama. Some collections from Belize and El Salvador may represent new species, but we include them here within the circumscription of *A. rupestre*. A single specimen from Oaxaca, Mexico (*Reko 3481d*) is widely separated from all other collections but otherwise seems to be typical *A. rupestre*, and this taxon may have a wider distribution in southern Mexico than herbarium specimens suggest. A specimen from Chiriquí, Panama (*Folsom 4804*, erroneously cited as 4803) was cited by Skog (1979) as *Phinaea albiflora* but is very similar to *A. rupestre*. Additional collections from near the same locality (*Dressler 4134*, 5132) have also been examined. These Panamanian collections fall well outside the range of *A. rupestre* and may represent a new species, but the available material is inadequate for a precise determination.

The nomen nudum "*Phinaea viscida* Denham ined." was cited by Wiehler (2002c) as a taxon from Chiapas, Mexico. This name was applied to plants of uncertain origin cultivated at Cornell University in the 1960s under their accession number G-889 but was never validly published. Photographic slides (duplicated at US) and a herbarium specimen made from this living ma-

terial at Cornell in 1966 (*Stone 218*) suggest that this taxon probably represents *Amalophyllon rupestre* although its caulescent habit and long-petiolate leaves are unusual for this species, particularly in specimens from Chiapas. These characters may be artifacts of cultivation (see also discussion under *A. clarkii*) as another collection shows significant morphological differences between specimens made from wild plants (*Moore 8196*) and those pressed from cultivated material of the same collection (*Moore 8196 bis*), suggesting that the vegetative morphology of this and other species may vary considerably due to environmental factors. Observations of *A. rupestre* in the wild (Myhr 2007) and in cultivation (Boggan pers. obs.) also suggest a high degree of phenotypic plasticity in vegetative characters.

Representative specimens. Belize—Cayo: Blue Hole National Park, 2006, *Myhr RM2006-01*, cultivated at the Smithsonian Institution, 3 Dec 2007, *Skog & Boggan 8271* (SEL, US); Caves Branch, Mountain Cow hill, 25 Jul 1976, *Whitefoord 1120* (BM), 3 Aug 1976, *Whitefoord 1206* (BM, MO). El Salvador—Ahuachapán: San Francisco Menéndez, El Corozo, Mariposario, zona “Los Sánchez”, 150 m, 15 Aug 2000, *Rosales 1315* (MO); San Benito, al E del camino de los Aguilares, 7 Aug 1992, *Sandoval & Chinchilla 557* (MO, US); La Libertad: Salvador, 9 km northeast of La Libertad, 200 m, 15 Aug 1938, *Worth et al. 8848* (K, UC, US); Sonsonate: Cantón y caserío Las Higueras, 580 m, 30 Jul 1989, *Reyna 1451* (F, MO, US). Guatemala—Alta Verapaz: Barranca del Rubelcruz, 3000 ft, Sep 1886, *Tuerckheim 725* (GH, K, US); Chimaltenango: lower and middle southwestern slopes of Volcán Fuego, above Finca Montevideo, along barranco Espinazo and tributary of Río Pantaleón, 1200–1600 m, 20 Sep 1942, *Steyermark 52121* (F, US); Escuintla: on dripping rocks painted with quetzal, km 47–48 on Ruta Nacional above Escuintla, 700 m, 3 Nov 1959, *Moore & Cetto 8196* (BH, US), cultivated at Cornell University, Aug 1962, *Moore & Cetto 8196 bis* (BH). Honduras—Ocotepeque: El Agua Caliente river, vicinity Guatemala and Honduras border, 900 m, 3 Sep 1975, *Molina & Molina 31034* (F, MO, PH). Mexico—Chiapas: 6–8 km NE of Huixtla along road to Motozintla, Mpio. of Huixtla, 200 m, 16 Nov 1971, *Breedlove & Smith 22538* (DS, MEXU), 6 Oct 1972, *Breedlove 28522* (DS, MO); Cerro Vernal, 21 km south of Tonalá, Mpio. of Tonalá, 750 m, 5 Oct 1974, *Breedlove 38137* (DS); above Finca Cuxtepec, Mpio. of Angel Albino Corzo, 1380 m, 11 Aug 1981, *Breedlove 52100* (CAS, MO); slopes of Río Cuxtepec, along stream below Fin-

ca Cuxtepec, Mpio. of Angel Albino Corzo, 900 m, 12 Aug 1981, *Breedlove 52135* (CAS, MEXU); between Finca Cuxtepeque and Finca Cabañas, Mpio. Angel Albino Corzo, 1100 m, 5 Nov 1988, *Breedlove & Daniel 71151* (CAS); 10 km NNE of Huixtla, 300 m, 26 Nov 1988, *Breedlove 71509* (CAS); Mpio. Acacoyagua, Ejida Las Golandrinas, lower slopes of Cerro Ovando, along road between Golandrinas and Los Cacaos, 800–900 m, 22 Aug 1996, *Croat 78543* (US); Fca. Fuarez, 12 Aug 1937, *Matuda 1764* (GH, K, NA, NY, US); between Mazapa and Motozintla, 1200 m, 19 Jul 1941, *Matuda 4877* (GH, NY); Municipio Angel Albino Corzo, finca Prusia south of Jaltenango, cultivated at Cornell University as G-889, 27 Jul 1966, *Stone 218* (BH); 4 mi N of Belisario along road from Huixtla to Motozintla, 3000 ft, 13 Aug 1972, *Webster et al. 17865* (DAV, DS); Oaxaca: Cafetal Calvario, Cerro Espino, Dist. Pochutla, 600 m, 20 Sep 1917, *Reko 3481d* (US). Nicaragua—Jinotega: along road from Hwy 3 through La Fundadora, between Las Camelias and La Salvadora, along small tributary of Río Jigüina, 1100–1150 m, 31 Oct 1979, *Stevens & Grijalva 15311* (MO, US), 28 Sep 1982, *Stevens et al. 21830* (US).

Amalophyllon sp. A.

Several collections from Panama probably represent a new species. This taxon is similar to the Ecuadorean species *A. clarkii* in its small size, minute flowers, and elliptic to lanceolate leaves with purplish leaf veins, but the leaves are more shallowly serrate and the flowers are described as white, pink, or orangish.

Representative specimens. Panama—Coclé: NE slopes of Cerro Caracoral, N rim of El Valle, 2700–2900 ft, 4 May 1981, *Sytsma et al. 4339* (MO); hills N of El Valle de Anton, 14 Aug 1971, *Wiehler 71251* (SEL, US); Panamá: trail to top of Cerro Pelado, 1000 m, 16 Jun 1979, *Antonio 1109* (MO, US).

Phinaea

Phinaea Benth., in Benth. & Hook.f., Gen. Pl. 2: 991, 997. 1876. LECTOTYPE: *Phinaea albolineata* (Hook.) Benth. ex Hemsl. Lectotypified by C.V.Morton & D.L.Denham, Taxon 21: 676. 1972.

Distribution. Three widely disjunct species in Mexico (*P. multiflora*), Cuba and Haiti (*P. pulchella*), and northern South America (*P. albolineata*).

Comments. *Phinaea albolineata* (or possibly a related species, see below) was included in recent phylogenetic analyses (Smith et al. 2004,

Roalson et al. 2005b, Roalson et al. 2008) which place it in a clade sister to *Monopyle*. A “particularly close affinity” between these two genera was proposed by Beaufort-Murphy (1983) on the basis of seed morphology. Although the two genera differ in numerous morphological characters, they both have fleshy fruits. Species previously placed in *Phinaea* that lack such fruits are here removed to the genus *Amalophyllon* (see above). As circumscribed here, *Phinaea* now contains only three or possibly four widely disjunct species. There are also some described taxa (see below under incertae sedis) that may belong in *Phinaea* but require further study.

Phinaea differs from both *Niphaea* and *Amalophyllon* most prominently in having pedicels erect in fruit; valves fleshy at dehiscence, opening broadly, and sticky seeds adhering to the valves after dehiscence. The plants are generally distinctly pubescent and the leaves sometimes have silvery veins. The nectary is usually described as absent and is not easily observed on pressed material but dissections of living material of both *P. albolineata* and *P. multiflora* revealed an annular nectary, albeit much reduced and apparently producing no nectar (Boggan pers. obs.). An early illustration (Hooker 1858) of *N. albolineata* var. *reticulata* Planch., a synonym of *P. albolineata*, also appears to show an annular nectary. Although the flowers of pressed specimens are difficult to distinguish from those of *Niphaea* and *Amalophyllon*, on living plants they are quite distinctive; *P. albolineata* has a short but distinct tube and zygomorphic flowers, and *P. multiflora* has cup-shaped flowers (rather than broadly spreading lobes).

Phinaea albolineata (Hook.) Benth. ex Hemsl., Biol. Cent.-Amer., Bot. 2: 472. 1882. BASIONYM: *Niphaea albo-lineata* Hook., Bot. Mag. 73: pl. 4282. 1847. TYPE: Colombia—Norte de Santander: near La Laguneta, Ocaña, Jul 1845, W. Purdie s.n. (Holotype: K; Isotypes: P, MPU).

Niphaea albo-lineata var. *reticulata* Planch., Fl. Serres Jard. Eur. 8: 201, pl. 823. 1853. TYPE: no specimens seen, probably typified by illustration. *Niphaea argyroneura* Planch. & Linden ex Planch., nom. nud. pro syn., Fl. Serres Jard. Eur. 8: pl. 823. 1853. *Phinaea albolineata* var. *reticulata* (Planch.) Hemsl., Biol. Cent.-Amer., Bot. 2: 472. 1882.

Distribution. Colombia (Norte de Santander), Brazil (Pará).

Comments. This species was originally described (possibly from cultivated material) from

Norte de Santander, Colombia but we have seen no collections from this region. Material of unknown origin cultivated at the Smithsonian Institution as *Phinaea albolineata* and included as such in molecular and morphological analyses (Roalson et al. 2005a) is virtually indistinguishable from the original illustration and description of *P. albolineata*. However, some or all cultivated material may be derived from a recent collection from Pará, Brazil (Plowman 8457). Judging from its distance from the type locality, this collection may represent a new species but is otherwise similar to *P. albolineata*, and we treat it here under this species. More collections from both localities are needed to determine the correct disposition of this collection. The nomen nudum “*Phinaea brasiliensis* Wiehler ined.” (Wiehler 2002c) may correspond to the Plowman collection, which is the only collection of this genus we have seen from Brazil.

Representative specimens. Brazil—Pará: Mpio. Conceição do Araguaia, range of low hills ca. 20 km W of Redenção, near Córrego São João and Troncamento Santa Teresa, 350–620 m, 8 Feb 1980, Plowman et al. 8457 (GH, NY, SEL, US), cultivated at the University of Chicago, 16 Oct 1980, Schroeder s.n. (US), cultivated in the Smithsonian greenhouses as USBRG 80-288, 1982, Skog s.n. (US). Origin unknown: Cultivated in the Smithsonian greenhouses as USBRG 02-150, 21 November 2002, Skog & Boggan 8263 (US).

Phinaea multiflora C.V. Morton, Bull. Misc. Inform. Kew 1938: 292. 1938. TYPE: Mexico, Guerrero: Vallecitos, District Montes de Oca, 24 Jul 1937, G.B. Hinton et al. 10626 (Holotype: K; Isotypes: BM, F, GH, MEXU, MO, NY, US).

Distribution and ecology. Mexico (Guerrero, Jalisco, Michoacan, Nayarit, Oaxaca, and Sinaloa) at 250–1555 m.

Comments. This is the most widespread and most commonly collected member of the genus, and is moderately variable. It is possible that *Niphaea cupreo-virens* Lem. (see incertae sedis) is an earlier name for this taxon, but the original description is inadequate to make this determination, and we have found neither illustrations nor specimens of *N. cupreo-virens*.

Representative specimens. Mexico—Guerrero: Plan del Carrizo, District Galeana, 650 m, 13 Oct 1939, Hinton et al. 14621 (GH, US); Jalisco: near Puerto El Triunfo 19 km WSW of Talpa de Allende along road to La Cuesta and Tomatlan, 1555 m, 11 Sep 1986, Anderson 64152 (CAS); Michoacan: Aquila, District Coalcoman,

400 m, 9 Aug 1941, *Hinton et al.* 15968 (K, LAM, MICH, NY, P, UC, US); Nayarit: 9.5 mi W of Tepic, 1000–1100 m, 11 Sep 1960, *McVaugh* 18953 (MICH, NY, US); Oaxaca: 10 km NE of Putla, 1020 m, 27 Aug 1988, *Breedlove* 69650 (CAS); Sinaloa: Mpio. Concordia, Sierra Madre Occidental, Panuco Road, 0.8 km N of Hwy 40 (Mazatlan-Durango Hwy) and ca. 1.5 km due N of Copala, 620 m, 31 Aug 1997, *Sanders et al.* 21032 (US). Origin unknown: Cultivated in the Smithsonian greenhouses as USBRG 02-151, 21 November 2002, *Skog & Boggan* 8261 (US).

Phinaea pulchella (Griseb.) C.V.Morton, *Brittonia* 9(1): 22. 1957. BASIONYM: *Niphaea pulchella* Griseb., *Cat. Pl. Cub.* 198. 1866. TYPE: Cuba. Exact locality unknown, 1860–1864, *C.Wright* 3069 (Holotype: GOET; Isotypes: BM, G, GH, K, MO, NY(3), P, S, UC, US).

Distribution and ecology. Cuba (Pinar del Río) on wet limestone rocks and cliffs.

Comments. This species is one of very few members of tribe Gloxinieae that occurs naturally in the West Indies, and is the only member of the tribe endemic to that region. We have not studied this species or its Haitian variety except to confirm that the fruit characters are consistent with its inclusion in *Phinaea*.

Representative specimens. Cuba—Pinar del Río: San Diego de los Baños, Aug 31-Sep 3, 1910, *Britton et al.* 6701 (NY, US); Sierra Organos, grupo del Rosario, on limestone rocks at Rio Palacios, near Nameyar, 13 Sep 1923, *Ekman* 17506 (K, NY, US); limestone hills, vicinity of Sumidero, 28–31 Jul 1912, *Shafer* 13400 (GH, MO, US).

Phinaea pulchella* var. *domingensis (Urb. & Ekman) C.V.Morton, *Brittonia* 9(1): 22. 1957. BASIONYM: *Niphaea domingensis* Urb. & Ekman, *Ark. Bot.* 22A(10): 72. 1929. TYPE: Haiti, Sud: Massif de la Hotte, Central Group, St.-Louis du Sud, Grand-Fond, 300 m, 1 Nov 1927, *E.L.Ekman* H 9213 (Holotype: W; Isotypes: A, F, G, GH, K, NY, S, US).

Distribution. Haiti (Sud), 300 m.

Comments. The type collection of this taxon is the only *Phinaea* we have seen from the entire island of Hispaniola, and if the specimen locality is not in error, this taxon may be extinct.

Niphaea

Niphaea Lindl., *Bot. Reg.* 27: Misc. 80. 1841. TYPE: *Niphaea oblonga* Lindl.

Distribution. Three described and an additional one or two undescribed species in Guatemala and southern Mexico.

Comments. *Niphaea* has traditionally been distinguished from *Phinaea* (including *Amalophyllon*) on the basis of floral characters (TABLE 1): anthers as long as filament, anther cells oblong, more or less parallel with locules confluent at apex. *Niphaea* can be additionally distinguished from both *Phinaea* and *Amalophyllon* by fruit characters: the fruit is a dry rostrate capsule with a fringe of stiff trichomes on the inner margins of the valves. Additional differences include having leaves that sometimes have purplish but never white or silver veins, and a chromosome count of $N = 11$ rather than $N = 13$ or 26, as found in *Phinaea* and *Amalophyllon*.

Wiehler (2002a) considered *Niphaea* to have 5 species. Of these, *N. peruviana* Wiehler has been transferred to *Nomophyle* (Roalson et al. 2005b), *N. saxicola* (Brandege) D.N.Gibson is here synonymized under *Amalophyllon rupestre*, and *N. cupreovirens* Lem. is considered to be incertae sedis (but probably a member of *Phinaea* s.s.). With our description of one new species and recognition of an additional undescribed species, we consider *Niphaea* to have four species.

Niphaea mexicana C.V.Morton, *Bull. Misc. Inform. Kew* 1936: 15. 1936. TYPE: Mexico, México: District of Temascaltepec, Nanchititla, 17 August 1933, *G.B. Hinton* 4544 (Holotype: K; Isotypes: BM, G, GH (2), NY, US (2)).

Distribution. Mexico (Guerrero, México, Oaxaca), collected at 600–1460 m.

Comments. One specimen from Oaxaca (*Reko* 3481a) is somewhat intermediate between *N. mexicana* and *N. oblonga* and may represent a hybrid or possibly a new species.

Representative specimens. Mexico—Guerrero: Sierra Madre del Sur, north of Rio Balsas, Distrito Adama, Temisco, Barranca de la Julia, 625 m, 3 Dec 1937, *Mexia* 8941a (UC); México: Volcan, District of Temascaltepec, 1460 m, 6 Aug 1932, *Hinton* 1277 (DS, GH, K, NY, US); District of Temascaltepec, Nanchititla, 22 Aug 1935, *Hinton et al.* 8203 (BM, EAP, F, GH, MO, NY, US); Oaxaca: Dto. Tehuantepec, Cerro Marimba, por Los Mangos, entrando por Rincón Bamba, al O de Salina Cruz, carr. a Pochutla adelante del Morro Mazatán, Mpio. Salina Cruz, 18 Sep 1987, *Martínez* 1043 (MEXU); Cafetal Calvario, Cerro Espino, Distr. Pochutla, 600 m, 20 Sep 1917, *Reko* 3481a (US).

Niphaea oblonga Lindl., Bot. Reg. 27: Misc. 80. 1841. Also 28: pl. 5. 1842. TYPE: Guatemala. Described from cultivation, originally collected by Hartweg in Guatemala, *Cult. Hort. Soc. London s.n.* (Holotype: K; Isotype: GH).

Distribution. Guatemala (Guatemala, Santa Rosa, Sololá) and Mexico (Chiapas), collected at 1500–1970 m.

Comments. Cultivated material of *N. oblonga* of unknown origin has been included in recent molecular analyses (Smith et al. 1997, Smith & Atkinson 1998, Zimmer et al. 2002, Roalson et al. 2005a). All material in cultivation is likely derived from a single collection from Chiapas, Mexico (*MacDougall s.n.*). This collection is the only known record of this species from Mexico but is otherwise an excellent match for specimens from Guatemala, as well as the original description and illustration.

Representative specimens. Guatemala—Guatemala: 1939, *Aguilar 203* (F); Santa Rosa: Cerro Redondo, 1500 m, Sep 1893, *Heyde & Lux 6140* (BM, GH, K, US); Sololá: 3 miles northwest of Panajachel on road to Solola, 1970 m, 3 Aug 1960, Beaman 3983 (GH); Panajachel waterfall near Panajachel, 1700 m, 18 Sep 1971, *Molina & Molina 26614* (F). Mexico—Chiapas: near Finca La Joya, Tapachula, 1500 m, *MacDougall s.n.*, cultivated at Cornell University as G-838, 11 Nov 1970, *Stone 1031* (US). Origin unknown: Cultivated in the Smithsonian greenhouses as USBRG 78-354, 1 Nov 1978, *Skog & Hodapp 5336* (US), 9 Jun 1988, *Skog & Folger 7564* (US), USBRG 93-038, 17 Nov 1994, *Skog 7680* (E, US, WAG).

Niphaea pumila J.K.Boggan & L.E.Skog, sp. nov. TYPE: Mexico, Sinaloa: Mpio. Concordia, Potrerillos y alrededores, ± 1500 m, 28 Aug 1988, *R. Vega A. et al. 2871* (Holotype: US). FIGURE 3.

Herbacea diminutiva sinaloensis in corollis albis a *Niphaeae ceterae* in partibus omnino parviores apprimae in laminis foliorum minus quam 4 cm longis et in limbis corollarum minus quam 1 cm in diametro differt.

Plant a diminutive epipetric herb; stem short, erect to ascending, 0–2 (–3) cm long, unbranched. **Leaves** opposite, subequal to unequal, usually congested at the stem apex; petioles 0.2–1 cm long, strigose, blade papery and fragile when dry, ovate to elliptic, (0.5–) 1–3 (–4) cm long, 0.5–1 cm wide, with 2–5 pairs of veins, margins crenate-serrate to lobed, green, often with purplish veins, base cuneate, frequently oblique, apex rounded to acute, strigose above and below. **Inflorescence** of axillary, solitary, epedunculate, ebracteolate flow-

ers; pedicels slender, 0.8–1.5 cm long, ascending, strigose; calyx lobes 5, elliptic-obovate, free at the base, subequal, 1–1.5 mm long, strigose; corolla 5-lobed, erect in the calyx, subrotate, white, limb 0.8–1.0 cm across, lobes entire, subequal, spreading broadly, slightly united at the base to form a very short tube, apices rounded, upper 2 lobes ca. 3 mm long \times 3 mm wide, lower 3 lobes ca. 4 mm long \times 3 mm wide, glabrous inside and outside; fertile stamens 4, inserted at the base of the corolla, filaments ca. 2 mm long, anthers white, apparently free, thecae ovoid, divergent, ca. 0.7 mm long; staminode not observed; nectary apparently absent; ovary half-inferior, ovoid, sparsely strigose, ca. 1 mm long, style glabrous, 2–3 mm long, stigma capitate to slightly bilobed. **Fruit** an ovoid rostrate capsule, ca. 4 mm long, loculicidally dehiscent; seeds not observed.

Phenology. Flowering and fruiting in August and September.

Distribution and ecology. Known only from the state of Sinaloa in Mexico, collected from wet cliffs and rocks along streams at 620–1500 m.

Comments. This diminutive species is one of the smallest known members of the Gesneriaceae. The type collection is smaller than the other collections cited and was collected at a higher elevation, but the specimens are otherwise similar. Scaly rhizomes have not been observed on specimens of this taxon but are probably present for at least part of the year. Although the anther thecae are ovoid and shorter than the anther filaments, because of the rostrate capsule we place this species in *Niphaea*. The stamen characters may be artifacts of the reduction in size of all parts of the plant, or may represent ancestral characters as the specialized stamen characters of the other known *Niphaea* species are autapomorphic within tribe Gloxinieae.

Paratypes. Mexico—Sinaloa: 1–2 km N of Copala on small mining road from Mexican Highway 40, Mpio. of La Concordia, 620 m, 10 Sep 1979, *Breedlove 43812* (CAS); Panuco, 700–750 m, 28–31 Aug 1935, *Pennell 20181* (PH, US); 35 miles E of Villa Union, creek and cliffs along highway, 3500 ft, 3 Sep 1967, *Oliver et al. 761* (MO); Mpio. Concordia, Sierra Madre Occidental, Panuco Road, 0.8 km N of Hwy 40 (Mazatlan-Durango Hwy) and ca. 1.5 km due N of Copala, 620 m, 31 Aug 1997, *Sanders et al. 21031* (US).

***Niphaea* sp. A**

Known from a single specimen, this distinctive taxon matches neither *Niphaea mexicana* nor *N. oblonga* and occurs outside the known range of either species. In its large leaves and

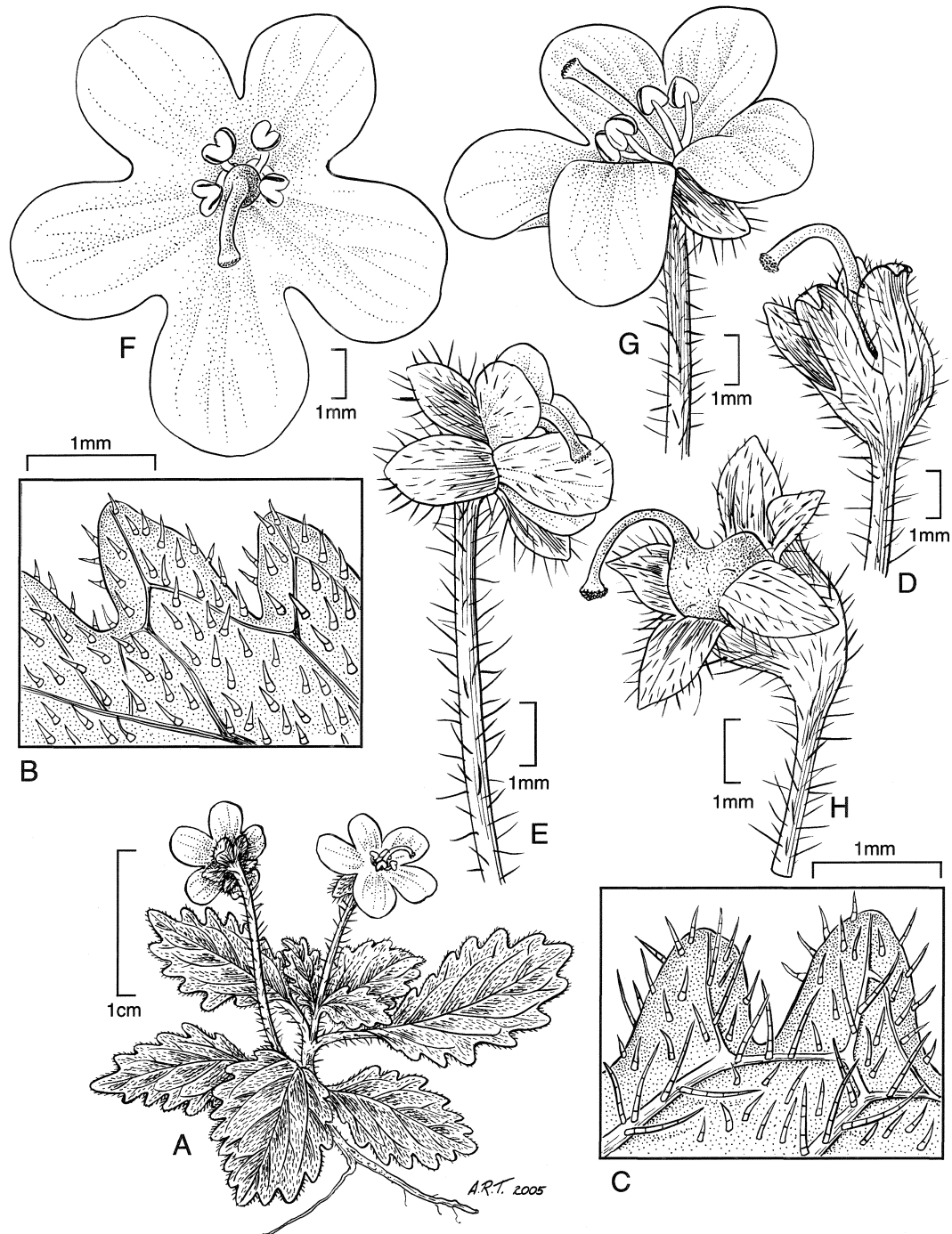


FIGURE 3. *Niphaea pumila*. A. Habit. B. Section of upper leaf surface and margin. C. Section of lower leaf surface and margin. D. Lateral view of flower with corolla removed. E. Lateral view of flower. F. Face view of flower. G. Lateral view of flower showing stamens and pistil. H. Fruit. A–C, E, G: drawn from *R. Vega A. et al.* 2871 (US). D, F, H: drawn from *D. Breedlove* 43812 (CAS).

flowers it most closely resembles *N. oblonga*. It is probably a new species but we have not seen sufficient material to describe it.

Representative specimen. Mexico—Sinaloa: Mpio. de Cosalá, Mineral de Nuestra Señora, 400 m, 23 Aug 1988, *Hernández & Hernández 806* (US).

EXCLUDED SPECIES

Niphaea peruviana Wiehler differs from all three genera in its fully inferior ovary and elongated cylindrical fruit that splits open for the entire length on the dorsal side. The fruit most resembles that of *Monopyle*, but it differs from that genus in other characters. Although not included in any molecular analyses, on the basis of morphology it seems to be most closely related to *Nomopyle dodsonii* (Wiehler) E.H. Roalson & J.K. Boggan (previously *Gloxinia dodsonii* Wiehler) and has therefore been transferred there recently as *Nomopyle peruviana* (Wiehler) E.H. Roalson & J.K. Boggan (Roalson et al. 2005a).

INCERTAE SEDIS

Niphaea cupreo-virens Lem., Ill. Hort. 7: 72. 1860. TYPE: unknown, no specimens or illustrations seen, described from cultivated material originally collected in Mexico in 1859 by Ghiesbreght. In the absence of any specimens, illustrations, or type locality, we cannot definitely associate this poorly described taxon with any of the above three genera. Lemaire's description of the anthers as "quadrilocellées" is puzzling, but from the description of the leaves as "molle, soyeuses par une très courte pubescence veloutée" and "dense velutino-tomentosulis," it seems likely to belong in *Phinaea* s.s., possibly as an older name for *P. multiflora* C.V. Morton.

Tapina villosa Gardner, Icon. Pl. 5: pl. 469. 1842. *Tapeinotes villosa* (Gardner) Walp., Repert. Bot. Syst. 2: 716. 1843. *Ligeria villosa* (Gardner) Hanst., Fl. Brasil. 8(1): 420. 1864. *Anethanthus villosus* (Gardner) Benth. ex Jacks., Ind. Kew. 1: 113. 1893. *Goyazia villosa* (Gardner) R. Howard, J. Arnold Arbor. 56(3): 367. 1975. *Gloxinia villosa* (Gardner) Wiehler, nom. illeg., non *Gloxinia villosa* (Lindl.) Mart. (1829), Selbyana 1(4): 387. 1976. Type: Brazil, Tocantins ("Goyaz"), Serra de Natividade, Gardner 3875 (Holotype: K; Isotypes: BM, CGE, E, F, FI-W, MANCH, OXF, P, W).

This poorly understood taxon, known only from the type collection, has yet to come to rest in any currently recognized genus, but it appears to be similar to *Phinaea albolineata*. Placed

most recently in *Goyazia* (Howard 1975) and *Gloxinia* (Wiehler 1976), the scaly rhizomes, villous leaves, thin annular nectary, and small white flowers with a short tube and subequal lobes suggest it belongs in *Phinaea*; but in lieu of a more careful examination of the type, the transfer is not made here.

ACKNOWLEDGMENTS

We would like to thank Alice Tangerini for the illustrations, Harold Robinson for his assistance with the Latin descriptions, Cynthia Morales for the use of her manuscript notes on *Niphaea* & *Phinaea* (for an unpublished revision of *Niphaea* with L.E. Skog as part of Smithsonian's Research Training Program), Christian Feuillet for commenting on the manuscript, and Ron Myhr for supplying living material and observations of *Amalophyllon rupestre* in Belize. We also thank curators of herbaria who loaned specimens for study, and in particular Roy Vick-er (BM) for searching for the type of *Niphaea caripensis* and other specimens. Michael Möller and one anonymous reviewer are acknowledged for their detailed reading and numerous helpful comments on the manuscript.

LITERATURE CITED

- Ayers, T.J. and D.E. Boufford. 1988. Index to the vascular plant types collected by H.H. Smith near Santa Marta, Colombia. *Brittonia* 40: 400–432.
- Beaufort-Murphy, H.T. 1983. The seed surface morphology of the Gesneriaceae utilizing the scanning electron microscope and a new system for diagnosing seed morphology. *Selbyana* 6: 220–422.
- Beddome, R.H. 1908. Gesneraceae, with annotated list of the genera and species which have been introduced to cultivation. *J. Roy. Hort. Soc.* 33: 74–100.
- Bentham, G. 1876. Gesneriaceae. Pp. 990–102 in G. Bentham and J.D. Hooker, *Genera Plantarum*, Vol. 2, Part 2. Lovell Reeve & Co., London, U.K.
- Brandege, T.S. 1914. *Plantae Mexicanae Purpusianae*, VI. Univ. Calif. Publ. Bot. 6(4): 63–67.
- Burt, B.L. and H. Wiehler. 1995. Classification of the family Gesneriaceae. *Gesneriana* 1(1): 1–4.
- Dates, J.D. 1986. The Gesneriad Register 1986. Check list of names with descriptions of intergeneric hybrids in the tribe Gloxinaeae [sic]. *The Gloxinian* 36(6) Suppl.: 1–12.
- Donnell-Smith, J. 1901. Gesneriaceae in Undescribed plants from Central America. *Bot. Gaz.* 31: 117–119.
- . 1903. *Enumeratio Plantarum Guatemalensis*, Vol. 6. H.N. Patterson, Oquawkae, Ill.
- Fischer, E. 2004. Scrophulariaceae. Pp. 333–432 in K. Kubitzki and J.W. Kadereit, eds. *The Families and Genera of Vascular Plants*, Vol. 7. Flowering Plants, Dicotyledons: Lamiales (except Acanthaceae including Avicenniaceae). Springer-Verlag, Berlin and Heidelberg, Germany.
- Fritsch, K. 1893–1894. Gesneriaceae. Pp. 133–185 in

- A. Engler and K. Prantl, eds. Die natürlichen Pflanzenfamilien, Vol. 4(3b). Wilhelm Engelmann, Leipzig, Germany.
- . 1916. Gesnerioideae, imprimis andinae Weberbauerianae et Kalbreyerianae. Bot. Jahrb. Syst. 54(Beibl. 119): 28–39.
- Gibson, D.N. 1972. Studies in American plants, IV. Phytologia 23: 334–342.
- . 1974. Gesneriaceae in Flora of Guatemala, Part X, Number 3. Fieldiana, Bot. 24: 240–313.
- Hemsley, W.B. 1882. Gesneriaceae. Pp. 471–489 in F. Godman and O. Salvin, eds. Biologia centrali-americana, Vol. 2. R.H. Porter and Dulau & Co., London, U.K.
- Hooker, W.J. 1858. *Niphaea albo-lineata*; var. *reticulata*. White-lined *Niphaea*; reticulated var. Bot. Mag. 84: pl. 5043.
- Howard, R.A. 1975. The genus *Anetanthus* (Gesneriaceae). J. Arnold Arbor. 56: 364–368.
- Lee, R.E. 1964. Additional chromosome numbers in the Gesneriaceae. Baileya 12: 159.
- . 1966. Additional chromosome numbers in the Gesneriaceae. Baileya 14: 142.
- and J.W. Grear. 1963. Additional chromosome numbers in the Gesneriaceae. Baileya 11: 131.
- Lindley, J. 1841. *Niphaea oblonga*. Bot. Reg. 27: Misc. 80.
- . 1842. *Niphaea oblonga*. Oblong snow-wort. Bot. Reg. 28: pl. 5.
- Martens, D. 1996. Intergenerics. African Violet Mag. 49(3): 44.
- Milewski, R.G. 1987. The Gesneriad Research Foundation study trip to Colombia. The Gloxinian 37(5): 17–22.
- Morton, C.V. 1937. Gesneriaceae in R.E. Woodson & R.J. Seibert, eds. Contributions toward a Flora of Panama, I. Ann. Missouri Bot. Gard. 24: 202–205.
- . 1957. Some West Indian Gesneriaceae. Brittonia 9: 18–24.
- Myhr, R. 2007. Gesneriad hunting in Belize. Gesneriads 57(1): 13–20.
- Poeppig, E.F. 1840. Gesneriaceae. Pp. 1–9, pl. 201–207 in E.F. Poeppig and S.L. Endlicher, Nova Genera et Species Plantarum, Vol. 3. F. Hofmeister, Leipzig, Germany.
- Roalson, E.H. and J.K. Boggan. 2006. New intergeneric names in the Gloxinieae (Gesneriaceae). Gesneriads 56(3): 34–41.
- Roalson, E.H., J.K. Boggan, and L.E. Skog. 2005a. Reorganization of tribal and generic boundaries in the Gloxinieae (Gesneriaceae: Gesnerioideae) and the description of a new tribe in the Gesnerioideae, Sphaerorrhizeae. Selbyana 25: 225–238.
- Roalson, E.H., L.E. Skog, and E.A. Zimmer. 2008. Untangling Gloxinieae (Gesneriaceae). II. Reconstructing biogeographic patterns and estimating divergence times among New World continental and island lineages. Syst. Bot. 33: 159–176.
- Roalson, E.H., J.K. Boggan, L.E. Skog, and E.A. Zimmer. 2005b. Untangling Gloxinieae (Gesneriaceae). I. Phylogenetic patterns and generic boundaries inferred from nuclear, chloroplast, and morphological cladistic data sets. Taxon 54: 389–410.
- Skog, L.E. 1976. A study of the tribe Gesnerieae, with a revision of *Gesneria* (Gesneriaceae: Gesnerioideae). Smithsonian Contr. Bot. 29: 1–182.
- . 1979. Flora of Panama, Family 175. Gesneriaceae. Ann. Missouri Bot. Gard. 65 [“1978”]: 783–996.
- . 2001. Gesneriaceae. Pp. 1114–1128 in W.D. Stevens et al., eds. Flora de Nicaragua. Angiospermas (Fabaceae-Oxalidaceae). [Monographs in Systematic Botany from the Missouri Botanical Garden, vol. 85, tomo II.] Missouri Botanical Garden Press, St. Louis, Missouri, U.S.A.
- Smith, J.F. and S. Atkinson. 1998. Phylogenetic analysis of the tribes Gloxinieae and Gesnerieae (Gesneriaceae): data from *ndhF* sequences. Selbyana 19: 122–131.
- Smith, J.F., S.B. Draper, L.C. Hileman, and D.A. Baum. 2004. A phylogenetic analysis within tribes Gloxinieae and Gesnerieae (Gesnerioideae: Gesneriaceae). Syst. Bot. 29: 947–958.
- Smith, J.F., J.C. Wolfram, K.D. Brown, C.L. Carroll, and D.S. Denton. 1997. Tribal relationships in the Gesneriaceae: evidence from DNA sequences of the chloroplast gene *ndhF*. Ann. Missouri Bot. Gard. 84: 50–66.
- Solereder, H. 1909. Zur Systematik einiger Gesneraceen-Gattungen, insbesondere der Gattung *Napeanthus*. Beih. Bot. Centralbl. 34: 431–439.
- Wiehler, H. 1975. The re-establishment of *Moussonia* Regel (Gesneriaceae). Selbyana 1: 22–31.
- . 1976a. A report on the classification of *Achimenes*, *Eucodonia*, *Gloxinia*, *Goyazia*, *Anetanthus* (Gesneriaceae). Selbyana 1: 374–404.
- . 1976b. New hybrid genera in the Gesneriaceae. Selbyana 1: 405–409.
- . 1983. A synopsis of the neotropical Gesneriaceae. Selbyana 6: 1–219.
- . 2002a. The history and biology of *Niphaea*. The Gloxinian 52(3): 21–25.
- . 2002b. Buzz or vibrational pollination in neotropical Gesneriaceae. The Gloxinian 52(3): 30–32.
- . 2002c. The history and biology of *Phinaea*. The Gloxinian 52(3): 33–37.
- Worley, P.J. 1979. \times *Niphimenes* (*Niphaea* \times *Achimenes*), a new hybrid combination in the Gesneriaceae. Selbyana 5: 195–196, figs. 1–8.
- . 1997. *Niphaea* intergeneric crosses—an experiment in flower form. The Gloxinian 47(1): 48–49.
- . 2002. Intergeneric hybrids with *Niphaea*. The Gloxinian 52(3): 25–26.
- Xu, Z. and L.E. Skog. 1990. A study of *Bellonia* L. (Gesneriaceae). Acta. Sci. Nat. Univ. Sunyatseni Suppl. 9: 95–107.
- Zimmer, E.A., E.H. Roalson, L.E. Skog, J.K. Boggan, and A. Idnurm. 2002. Phylogenetic relationships in the Gesnerioideae (Gesneriaceae) based on nrDNA ITS and cpDNA *trnL-F* and *trnE-T* spacer region sequences. Amer. J. Bot. 89: 296–311.